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Comparison of behavioral patterns of hilltopping butterflies on the summit, subsummit and slope of two mountains on the boundary between Osaka and Nara Prefectures, Central Japan

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Abstract New categories of hilltopping/hilltopper supplementing the traditional one in the sense of Shields (1967) can be defined by examining the proportions of each behavioral category practiced by hilltopping males of 15 butterfly species on the summit, subsummit and slope of Mt Nijo and Mt Katsuragi, Central Japan from April to October in 2002. Proportions were evaluated based on percentage of male behavioral patterns, Perching, Flying, Intra- and Inter-specific fights, Foraging, etc., observed in a total of 22 and 26 5-m radius observation circles scattered on each altitudinal subzone of Mts Katsuragi and Nijo, respectively, during 5 min census periods. Five different types of hilltopping behavior, Types A1, A2, B, C1 and C2, were separated in this study. Species from Type A1, the narrow sense or "classical" hilltopping type, used hilltops only for mating. *Papilio machaon*, *Luehdorfia japonica*, *Argyreus hyperbius*, *Cynthia cardui*, *Vanessa indica*, the overwintering adult of *Nymphalis xanthomelas*, *Hestina japonica* and *Lampides boeticus* belonged to Type A1. Type A2 species such as *Papilio xuthus*, *Papilio bianor* and *Papilio helenus* were identical in purpose to Type A1 but never perched and had a patrolling route running through the slopes. Type B species, such as *Parnara guttata*, used hilltops for a combination of 3 purposes: nectaring, mating and as a short stop during their migrations. In Type C1 species, such as *Libythea celtis* and the summer adult of *N. xanthomelas*, hilltops were used as temporary habitats during aestivation, including reproductive diapause for *L. celtis*, to avoid summer heat in lowland areas. Finally, in Type C2 species, such as *Colias erate* and *Lycaena phlaeas*, hilltops were not only used as temporary habitats during aestivation but other purposes were also associated: breeding on foodplant in the case of *C. erate*, nectaring and mating.

Key words Butterfly, hilltopping, hilltop, territoriality, Mt Katsuragi, Mt Nijo, Japan.

Introduction

Hilltopping or the congregation of certain insect species belonging to different orders such as Coleoptera, Diptera, Hymenoptera, Lepidoptera and Orthoptera on hilltops, mountaintops (*e. g.* Shields, 1967; Scott, 1968; Alcock and Carey, 1988), ridgetops (*e. g.* Alcock and Smith, 1987), cliff-tops (Shapiro, 1979) or even on the highest portion of a nearly flat habitat (Baughman and Murphy, 1988), has long been the focus of many studies concerning its potential adaptive significance (Ehrlich and Wheye, 1986; Baughman *et al.*, 1988; Singer and Thomas, 1992). For certain species, these aggregations are composed of males and females and would act as thermal refugia for montane grasshoppers during winter time in South Africa (Samways, 1990) or would serve as gathering places for hibernating Coccinellidae, Chrysomelidae beetles or for aestivating Noctuidae moths (Shields, 1967).

In butterflies, the most commonly cited and agreed hypothesis is that hilltops are mating rendezvous places for low density species (Shields, 1967; Scott, 1968) or species whose receptive females are diffusely distributed in space and time (Alcock, 1983; Rutowski and Alcock, 1989). However, Dennis and Dennis (2006) recently suggested that hilltopping can

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be generated by other purposes than mating, such as peaks being used during the autumnal return migration of the nymphalids, *Inachis io* and *Aglais urticae*, which would explain the presence of a non-breeding generation of those species on certain British hilltops. It is therefore useful to explore the possibility of categorizing hilltoppers based on their observed behaviors. How far behavioral patterns, *i. e.* proportions of different behaviors, of hilltopping males are similar among a series of different butterfly species on the same and different hilltops and at different altitudinal levels on the hill, such as summit, subsummit and slope, has not yet been investigated.

In this paper, by using the hilltopping butterfly fauna determined in our previous study (Navez and Ishii, 2007) on 2 mountains on the boundary between Osaka and Nara, Central Japan, we try to define broader significances to the notion of hilltopping and hilltopper.

Study sites and methods

Study sites and schedule

The study was carried out on two mountains belonging to the Kongo-Ikoma mountain range at the frontier between Osaka and Nara Prefectures, Central Japan, Mt Katsuragi or Mt Yamato-Katsuragi (960 m alt) and Mt Nijo with 2 peaks separated by a saddle (431 m alt): Odake (517 m alt) and Medake (474 m alt) for 75 days from 8 April to 16 October in 2002. We fixed 22 and 26 5-m radius observation circles at different altitudinal levels on Mt Katsuragi and Mt Nijo, respectively, and the frequency of behaviors for any encountered butterfly species within each circle during 5 min census periods was recorded. The observations were made during 5 sessions per census day (every two hours) from 8h30 or 9h00 to 18h00 as a rule. Besides, on Mt Katsuragi, summit and subsummit were censused on different days and, on Mt Nijo, one day was spent only on Medake summit plus subsummit (10 circles), another day only on Odake summit plus subsummit (10 circles) and still another day covering only the slope transect (6 circles). For the slope transect on Mt Nijo, 3 sessions/day were made, with early beginning or later beginning census days, in alternance, in order to compensate for missing periods and to get the full range schedule. The location of study sites and observation circles, and vegetation were described in Navez and Ishii (2007).

Definition of each behavioral pattern

In this study, behavioral patterns were defined as follows: "Perching" refers either to a butterfly resting on a substratum and investigating any passing-by object in an aggressive way or not, then resuming its former position or just to a resting or basking individual. In the latter case, there is some ambiguity about whether or not this constitutes a kind of mating behavior. "Flying" consists either of a butterfly patrolling many times or once a specific route and investigating any passing-by or resting butterfly or of a butterfly just passing without any stop. The latter case is ambiguous as to whether or not it constitutes a mate-locating behavior. "Fighting" comprises investigative, non-aggressive chases, and the vertically ascending or horizontal aggressive bouts between two individuals of the same (*i. e.* intraspecific) or different (*i. e.* interspecific) species. In the text, the terms "chase" and "fight" are used indiscriminately, as synonyms, though "chase" was more appropriate for non- or slightly aggressive species. "Total chases or fights" comprised both intra- and interspecific contests. "Foraging" means nectaring on flowers. "Courtship" is the stereotyped display of male and female before mating but, in this study, in copula mating pairs were also included in this category. "Roosting" refers to any motionless butterfly found, in early morning or late in the afternoon, settled down on vegetation, with particular postures, for sleep.

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"Puddling" is any individual or group drinking on mud. Puddling, roosting and foraging are not mating behaviors.

As a method for categorizing hilltoppers, the presence of certain behaviors in a relatively high proportion to other behaviors is characteristic of hilltopping behavior with a specific purpose and therefore of a specific type, depending on which altitudinal zone it happens at. When comparing the number of perching and flying records in each particular zone, other behaviors such as fighting were eliminated from the total sample size, in order to use the binomial test based on an expected ratio 0.5.

Results and discussion

In a previous paper (Navez and Ishii, 2007), we divided hilltopping butterflies into real hilltoppers and controversial ones. From the following results based on behavioral patterns, we propose a new hilltopper classification.

Species accounts

1. *Papilio machaon*

In Nijo 2002 (Figs 1c–d), on both Odake and Medake summits, intraspecific fights occurred and a much higher percentage of flying than perching records were observed ($p<0.001$, $N=335$ in Odake and $p<0.001$, $N=423$ in Medake, by binomial tests). This species was thus a territorial, dominant patroller there. No foraging was seen on Odake summit and there were few foraging records on Medake summit relative to the subsummit and slope ($p<0.001$, $N=584$ and $p<0.01$, $N=583$, by Chi-square tests). Besides, no fights were observed on the slope and only a small proportion of intraspecific ones on the subsummit compared to the summits, though this was significant only for Odake ($p>0.05$, $N=584$ for Medake; $p<0.05$, $N=623$ for Odake, by Chi-square tests) (Figs 1c–f). When considering all fights, including interspecific ones, the tendency remained the same ($p>0.05$, $N=584$ for Medake; $p<0.01$, $N=623$ for Odake).

In Katsuragi 2002 (Figs 1a–b), intraspecific fights occurred and there was a much higher percentage of flying than perching on the summit ($p<0.001$, $N=733$, by binomial test) while, on the subsummit A (SubA), foraging was much more important ($p<0.001$, $N=1360$, by Chi-square) and there were far less intraspecific fights or total fights ($p<0.001$, $N=1360$, Chi-square tests) and less perching ($p<0.05$, $N=1360$, Chi-square test). This species was thus a territorial, dominant patroller on the summit and SubA. It should be mentioned that 2 females were seen ovipositing on the summit and SubA, respectively, but, since foodplants were rather rare on the broad hilltop (Navez and Ishii, 2007), the main breeding site should be downslope.

As a conclusion, on both mountains, *P. machaon* exhibited a "classical" behavioral pattern for a hilltopper according to criteria evoked in Shields (1967): the typical behavioral activities of summit males were territorial perching or patrolling behavior, with intra- and interspecific aggression displayed toward other butterflies. However, the present study added far more precision to that of Shields in two aspects. First, it compared subsummit and slope behavioral patterns with summit ones and showed the divergences of patterns among those three subzones. Second, it quantified the proportions of the different behaviors observed. Our results offer thus only a convergence with Shields'. Indeed, in spite of totally different methods and approach, they support the conclusions of Shields'. In the following accounts, we will use "in the sense of Shields" to express this convergence. This species was also referred to as a hilltopper by Fukuda *et al.* (1982), Hiura (1976), Isobe (1980, cited in

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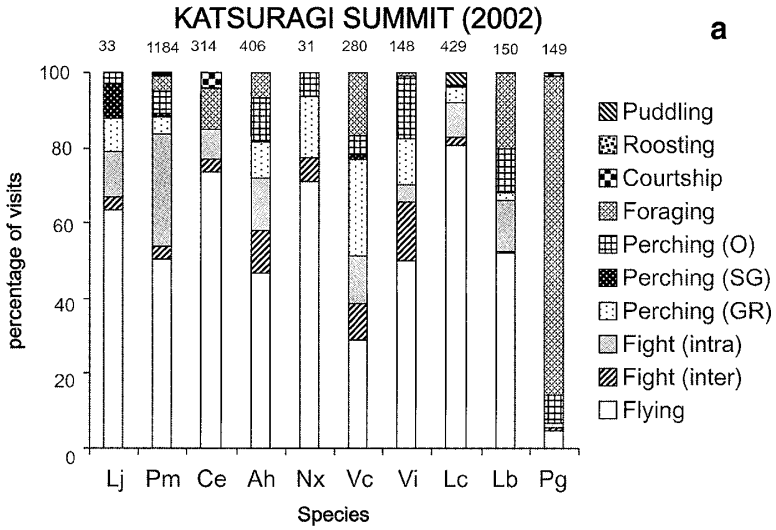

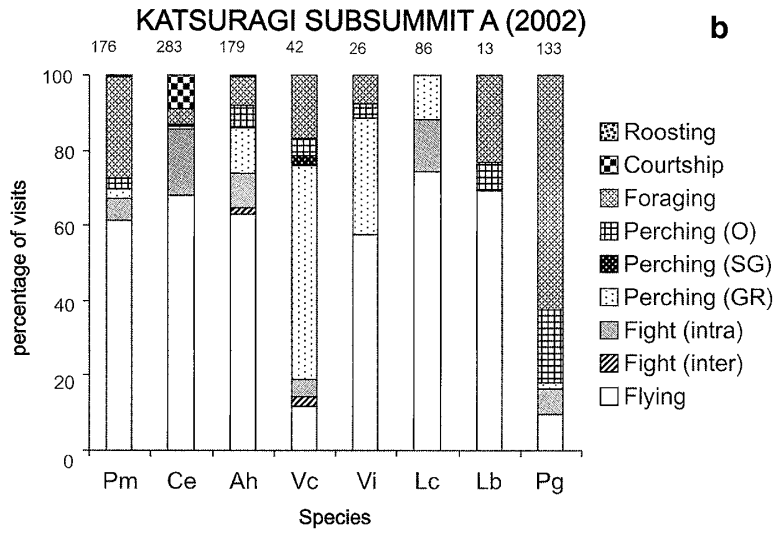

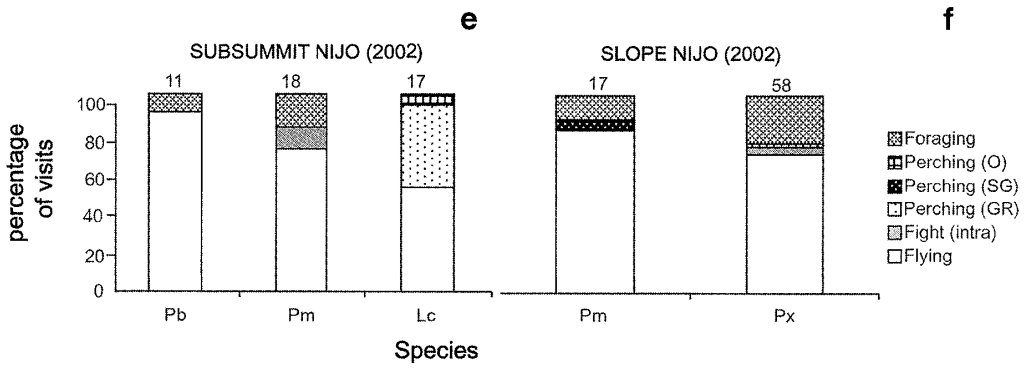

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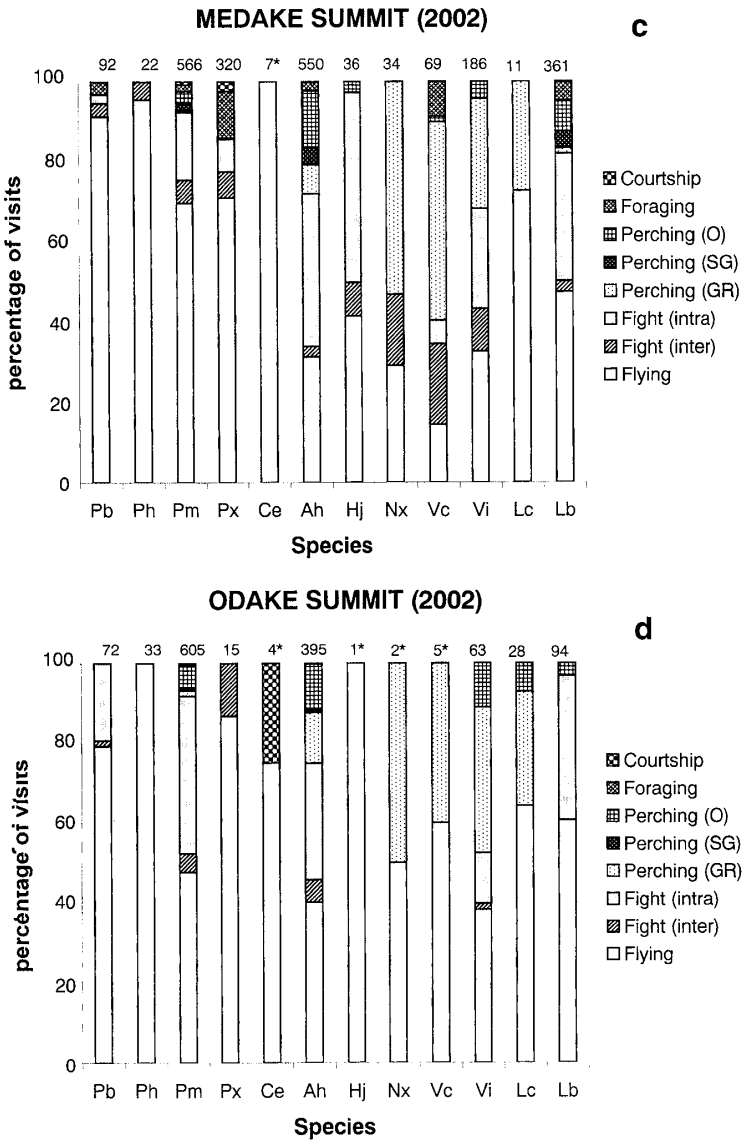

Figs 1a–f. Male behavioral patterns of the hilltopping species from Mt Nijo and Mt Katsuragi in 2002 on each subzone (but no slope data for Mt Katsuragi 2002). On the slope and subsummits, only species with ≥10 records there were considered. Sample sizes are indicated above each bar of the histogram. * =too small sample size on Medake and/or Odake summits but the species is still mentioned in order to highlight any difference in the distribution on both peaks. GR=ground; SG=short grass; O=others; intra=intraspecific; inter=interspecific; "perching" comprises here basking and resting records too (=exhaustive definition); "courtship" also includes mating pairs data. Ah=*A. hyperbius*, Cc=*C. cardui*, Ce=*C. erate*, Hj=*H. japonica*, Lb=*L. boeticus*, Lc=*L. celtis*, Lj=*L. japonica*, Nx=*N. xanthomelas*, Pb=*P. bianor*, Pg=*P. guttata*, Ph=*P. helenus*, Pm=*P. machaon*, Px=*P. xuthus*, Vi=*V. indica*.

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Watanabe, 1988), Kawazoé and Wakabayashi (1976), Scott (1986) in Northern America, Shields (1967) in Southern California and Takahashi (1966, cited in Watanabe, 1988).

2. *Papilio xuthus*

In Nijo 2002 (Figs 1c–d), on Medake and Odake summits, intra- and/or interspecific aggressive chases were observed, but no perching, except as a trace. Only very few records were seen on Odake. This species was thus a territorial patroller on both peaks and not a hilltopper on Odake. No foraging was reported on Odake summit but a high proportion of foraging occurred on Medake summit (Figs 1c–d), though somewhat less than on the slope ($p<0.05$, $N=378$, Chi-square) where nearly no fights at all were observed (Fig. 1f). Only 8 records were reported on the subsummit (6 flying, 2 roosting and, thus, no fights) but 58 on the slope, with ca 70% of flying individuals. Courtships were seen only on the summit on Medake.

As a conclusion, this species was a hilltopper on Mt Nijo in the sense of Shields (1967) but a weak one since many individuals were also seen patrolling on the slope of Mt Nijo. No reference in literature cites this species as hilltopper.

3. *Papilio helenus*

In Nijo 2002 (Figs 1c–d), some fights occurred only on Medake summit but they were interspecific, and P. helenus was not the aggressive species. Otherwise, the only behavior observed on both summits was flying. This species was thus a non territorial patroller there. No records occurred on the slope and only 7 records, flying, on the subsummit. No foraging nor courtships were witnessed on the whole mountain, at least along the transect route.

As a conclusion, it was a hilltopper on Mt Nijo in the sense of Shields (1967). It was also reported as a hilltopper in Kiritani *et al.* (1984), Kawazoé and Wakabayashi (1976) and Suzuki *et al.* (1985). *P. helenus*, like *P. xuthus*, should also normally be classified as a weak hilltopper because its mid-summer patrolling route tracks the distribution of its seashore foodplants (*e. g. Zanthoxylum ailanthoides* and *Evodia meliifolia* (Rutaceae)) in bright forest edges all over the plain including slopes of low mountains (Fukuda *et al.*, 1982). The absence of *P. helenus* on the slope of Mt Nijo may simply be due to the absence of foodplants there, at least along the transect route used.

4. *Papilio bianor*

In Nijo 2002 (Figs 1c–d), aggressive intraspecific chases were seen on the summits of Medake and Odake but especially on the latter peak ($p<0.001$, $N=164$, Chi-square). No perching records were observed and 80% or more of total visits were flying. This species was thus a territorial patroller on both summits of Mt Nijo. No foraging was seen on Odake summit. No fights occurred on the subsummit and a somewhat higher proportion of foraging was found there than on the summit of Medake, though the difference was not statistically significant ($p>0.05$, $N=103$, Chi-square). Only 1 record, a flying male, was reported on the slope on September 8.

As a conclusion, it is a hilltopper on Mt Nijo in the sense of Shields (1967). No hilltopping accounts were found in the literature but indirect arguments exist, such as the well known hilltopping habit of most species in the genus *Papilio* (Shields, 1967; Scott, 1968). *P. bianor* should be a weak hilltopper on the same basis as suggested above for *P. helenus*.

5. *Luehdorfia japonica*

In Katsuragi 2002 (Fig. 1a), aggressive intraspecific fights occurred on the summit and the

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proportion of flying was higher than the perching one ($p<0.05$, $N=28$, binomial test). This species was thus a territorial percher and patroller on the summit, with a dominance of the latter behavior. Only 1 record, flying, was found on SubA on April 27 and, though not shown in Fig. 1b, 14 records on SubB, C, D, namely 12 flying, 1 perching, 1 foraging and no fights. There was one record of copulation on the summit on April 19 2005, at 10: 34 in Circle SUM6' (see Navez and Ishii, 2007). A male was continuously present in that circle from 10: 17 to 10: 34 on the day and alternated a circular patrolling route along a row of pine trees and above stone benches with perching within the circle. At 10: 34, a female arrived in the circle and the male darted directly at her, then after meeting in the air they immediately settled down on the ground and formed an in copula pair. Then, 10 seconds later, the pair flew away to the canopy of one of the pine trees and settled on a canopy branch.

As a conclusion, it was a hilltopper in Katsuragi in the sense of Shields (1967). It is also considered as hilltopper by Fukuda *et al.* (1982) and Natsuaki (1996). Our behavioral arguments and the marking experiment results of Natsuaki (1996) and Natsuaki and Takeuchi (1999) remove the doubt from our previous paper (Navez and Ishii, 2007). Two comments can be made. First, in Matsumoto (1987), males were only described as non territorial patrollers in Kanazawa City suburb, exhibiting non aggressive investigative chases when encountering conspecific males or other butterfly species. In Natsuaki and Takeuchi (1999), they were territorial patrollers in Toyono-cho (northern Osaka Prefecture), though there was mention of 1 "resting" male on a dead leaf on the hilltop. In our study, aggressive perching behavior was shown by males, though the main behavior was patrolling. Second, in Natsuaki and Takeuchi (1999), the host plant occurred at the foot of the hill. In contrast, on Mt Katsuragi, it was concentrated in a subsummit area (*ca* 100 m lower than the hilltop), which creates some ambiguity concerning the hilltopper status of territorial males on the summit and about the definition of hilltopping.

6. *Argyreus hyperbius*

In Nijo 2002 (Figs 1c–d), on both summits, aggressive intraspecific chases occurred and flying and perching proportions were roughly equal in Medake ($p>0.05$, $N=314$, binomial test) but more flying occurred on Odake ($p<0.001$, $N=256$, binomial test). This species was thus a territorial percher and patroller on both peaks, but with more patrolling on Odake. A very small proportion of summit foraging occurred on Medake. One mating pair was found on Medake summit on August 15 and one courtship on Odake summit on July 20. Very few data were reported on the subsummit, namely 5 records: 2 flying males, 2 perching males, 1 foraging female and no fights. And only 1 record, a flying male, was reported on the slope. On Medake and Odake summits, only 0.4% ($N=552$) and 1.5% ($N=401$) of female visit records were obtained on the two peaks, respectively.

In Katsuragi 2002 (Figs 1a–b), on the summit and SubA, aggressive intraspecific fights were present and, even if more flying than perching occurred ($p<0.001$, $N=278$, on the summit; $p<0.001$, $N=146$, on SubA; binomial tests), the proportion of perching was not negligible.

Therefore, as on Mt Nijo, *A. hyperbius* was a territorial percher and patroller on the summit and SubA. Nearly the same relative proportions for intraspecific fights ($p>0.05$, $N=585$, Chi-square), perching ($p>0.05$, $N=585$, Chi-square) and foraging ($p>0.05$, $N=585$, Chi-square) were found on the summit and SubA. The hilltop perceived by *A. hyperbius* ("biological hilltop") would thus be wider than, for instance, *P. machaon*, *i. e.* would include more of the subsummit (=wide summit). However, when considering the total fights, including interspecific ones, the proportion on the summit was much higher than on the SubA ($p<0.001$, $N=585$, Chi-square). It should be noted that, in 2001, one courtship rejection by

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the female was seen in circle SUB20 on 27 June. On the summit, only 1.5% (N=340) of female visit records were obtained in 2001 and 2.2% (N=415) in 2002.

As a conclusion, on both mountains, it was a hilltopper in the sense of Shields (1967). It is also referred to as a hilltopper in Fukuda *et al.* (1983) and Hiura (1976).

7. *Nymphalis xanthomelas*

In Nijo 2002 (Figs 1c–d), aggressive interspecific chases where it was the aggressive species occurred on Medake summit and the proportion of time spent flying there was smaller than that spent perching, though in a non significant way (p>0.05, N=28, binomial test). Therefore, it was a territorial percher on that summit or at least in spring, since there were no summer records of this species on Mt Nijo in 2002, possibly because the newly emerged summer individuals are migrants only to high altitude mountains (Hirukawa, 1997). As only 2 records were made on Odake summit, it seemed not to hilltop on that peak. However, several additional accounts of territorial perching there were obtained in 2003. For instance, on April 17 2003 at 13: 50 in Circle OS5, a male was perching on the mud path and continued to perch there until 14: 35. It twice attacked a flying *P. machaon* passing above the circle and, afterwards, resumed its former perching position in Circle OS5 or nearby OS4. On April 21 2003, at 13: 52, 2 males were territorial perchers at the same time on Odake summit, in Circles OS5 and OS1, respectively. Finally, on May 3 2003, at 15: 15, a male was perching in Circle OS5 and attacked individuals of *P. bianor*, *P. xuthus*, and *Graphium sarpedon*, while always resuming its perch after each attack. On Nijo 2002, there were only 2 flying males on the subsummit and no slope data. On Katsuragi 2002 (Figs 1a–b), interspecific fights where it was the aggressor occurred on the summit and both flying and perching occurred there in non negligible proportions, though with a dominance of flying (p<0.01, N=29, binomial test). It was thus a territorial percher and patroller on the summit. Only 9 records were reported on SubA (5 flying, 4 perching and no fights) and 7 records on Sub B, C, D (3 flying, 4 perching and no fights). Interspecific fights occurred on June 4 2002 at 15: 29 in Circle SUM6' of Katsuragi summit: a male was perching on a stone bench then on the muddy path and interacted aggressively with a flying individual of *C. erate*. After interaction it came back to its previous perch, then did some restricted circular patrolling within the circle and perched again on the path or bench. The same scenario repeated many times. On June 4 2004, in the same circle at 13: 16, a male was also perching on a stone table. It attacked a species of fly (Diptera) then resumed its former perching position. On the same day at 14: 33, it was still perching on the table and attacked 1 flying *C. erate* then perched back on the table. It also, spontaneously, frequently left its perch for a restricted patrolling flight within the circle and then perched back on the table or ground. It should be noted that, in spring 2003, on March 28, two males were also perching territorially in the same circle, continuously (at least for one male) from 11: 20 to 14: 00. Intraspecific aggressive interactions occurred between them.

As a conclusion, it was a hilltopper on both mountains in the sense of Shields (1967). It is also reported as hilltopper by Fukuda *et al.* (1983) and Hirukawa (1997). The proportion represented by flying on the summit was much higher on Mt Katsuragi than on Mt Nijo (p<0.01, N=67, Chi-square), for two reasons. First, since this species mostly concentrates its spring mate-locating activity in Circle SUM6', a circle not yet present in spring 2002, the proportion of perching and interspecific fights was surely underestimated. Incidentally, the fact that, on both mountains, no intraspecific fights were witnessed reflects the low density of population of this species on the hilltops. Second, in contrast with Mt Nijo, the summer generation was also observed on the hilltop and most individuals in summer were flying (19 flying, 7 perching, 2 interspecific fights). The interspecific fights, in association

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with territorial perching, observed on the summit on Katsuragi 2002 occurred on June 4 (*i. e.* summer generation) but copulation of this univoltine species seems to occur only in spring (*i. e.* overwintered generation) on hilltops (Fukuda *et al.*, 1983; Hirukawa, 1997). Hirukawa (1997) also reported similar territorial behavior on top of high mountains in Nagano Prefecture, namely more than 2000 m, in mid-summer. Since butterfly territoriality is always related to mating behavior (*e. g.* Baker, 1972; Kemp & Wiklund, 2001), the meaning of the summer aggressive chases on the hilltop is unclear. The same dilemma will be discussed for *L. celtis* on Mt Katsuragi (see below). Therefore, in a narrow sense, namely "aggregation on the summit for mating purpose", *N. xanthomelas* does not seem to be a hilltopper in the summer season.

8. *Cynthia cardui*

On Nijo 2002 (Figs 1c–d), intraspecific fights occurred on Medake summit and there was a very small percentage of time spent flying there, comparatively to perching ($p<0.001$, $N=45$, binomial test). Only very few records were taken on Odake summit. This species was thus a territorial percher on Medake summit but did not hilltop on Odake summit. No records at all were taken on the subsummit and slope (Figs 1e–f).

On Katsuragi 2002 (Figs 1a–b), intraspecific fights occurred on the summit and subsummit. Flying and perching were roughly in equal proportions on the summit ($p>0.05$, $N=170$, binomial test), while the percentage of flying was far inferior on SubA ($p<0.001$, $N=32$, binomial test). Therefore, *C. cardui* was a territorial percher and patroller on the summit and territorial percher on SubA. Intra- and interspecific fights were more important on the summit than at SubA, though non-significantly ($p>0.05$, $N=322$, Chi-square tests). However, when lumping both types of fights, it became significant ($p<0.05$, $N=322$). Foraging occupied the same percentage on summit as at SubA ($p>0.05$, $N=322$, Chi-square).

As a conclusion, on both mountains, it was a hilltopper in the sense of Shields (1967). Reports of hilltopping also exist in Alcock (1984), Alcock and Gwynne (1988), Brown and Alcock (1990(91)), Fukuda *et al.* (1983), Pringle et al (1994), Scott (1986) and Shields (1967).

9. *Vanessa indica*

On Nijo 2002 (Figs 1c–d), on Medake and Odake summits, intraspecific fights occurred and flying and perching proportions were roughly equal ($p>0.05$, $N=120$ in Medake; $p>0.05$, $N=54$ in Odake; binomial tests). This species was thus a territorial percher and patroller on both summits. No foraging was seen on the summits. Almost no data were obtained on the subsummit (1 record: perching) and slope (2 records: 1 flying, 1 perching).

On Katsuragi 2002 (Fig. 1a), intraspecific fights occurred on the summit and there was a high proportion of flying and perching there. *V. indica* was thus a territorial percher and patroller on the summit. No fights happened on the SubA and more foraging was observed there than on the summit ($p<0.05$, $N=174$, Chi-square but $p>0.05$ by Fischer's Exact Test).

As a conclusion, on both mountains, it was a hilltopper in the sense of Shields (1967). It was also reported as a hilltopper in the same references as those cited for *C. cardui* and in Kawazoé and Wakabayashi (1976).

10. *Hestina japonica*

On Nijo 2002 (Figs 1c–d), on Medake summit, intraspecific aggressive chases and a very small percentage of perching compared to flying occurred ($p<0.01$, $N=16$, binomial test). This species was thus a territorial patroller on Medake. Since only 1 record was taken on

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Odake summit, it may not be a hilltopper there. No records were reported on the subsummit and slope on Mt Nijo (Navez and Ishii, 2007).

As a conclusion, it seemed to be a hilltopper on Medake, in the sense of Shields (1967). However, since this species pupates on the foodplant trees (*Celtis* spp., Ulmaceae) (Fukuda *et al.*, 1983), it should use the larval foodplant as a mate encounter site (according to Rutowski, 1991) instead of hilltopping. Indeed, male territories were reported on canopies of *Celtis* spp. and relatives in all parts of Japan, lowland, slopes and summits included (Fukuda *et al.*, 1983). Since no *Celtis* trees were present on Medake summit where *H. japonica* males were consistently territorial, day after day, on certain canopies (Quercus spp. (Fagaceae)) in summer, the hilltopping hypothesis cannot be, nonetheless, rejected. No reference in literature cites this species as a hilltopper.

11. *Libythea celtis*

On Katsuragi 2002 (Figs 1a–b), on the summit and SubA, intraspecific aggressive chases and a higher proportion of flying than perching occurred ($p<0.001$, $N=365$ on summit; $p<0.001$, $N=74$ on SubA; binomial tests). Perching was exclusively on the ground. This species was thus a territorial, dominant patroller there. Intraspecific chases or total chases including interspecific ones happened in more or less equal proportion on the summit and SubA ($p>0.05$, $N=515$, Chi-square tests), which recalls the "wide summit" pattern of *A. hyperbius* as mentioned above. A small proportion of puddling was observed on the summit. In Katsuragi 2001, a year of excessively high population density, 21% ($N=815$) of intraspecific aggressive fights, mostly spiral but sometimes also horizontal, took place on the summit, which is a much higher proportion than in 2002 ($p<0.001$, $N=1244$, Chi-square) and no fights occurred on the slope.

On Nijo 2002 (Figs 1c–e), no fights were observed on either summit or on subsummits and the proportion of flying was somewhat greater than that of perching on the 2 summits, though in a non significant way ($p>0.05$, $N=11$ in Medake; $p>0.05$, $N=28$ in Odake; binomial tests). It was thus a non territorial percher and patroller there. The sample size on the subsummit was more or less equivalent to that on the summit areas. Only 1 record of flying occurred on the slope. On account of the population size alone, *L. celtis* was discarded as a hilltopper on Mt Nijo. However, considering that the "biological hilltop" (see *A. hyperbius*) of *L. celtis* also includes the subsummit, there was a definite trend in the distribution to be biased towards that "broad summit".

In the North American libytheid, *Libytheana bachmannii*, a related species to *L. celtis*, showing dramatic seasonal changes in population density, males were, all year round, non territorial patrollers with no individuals perching aggressively (Rutowski *et al.*, 1997). In the case of *L. celtis*, not only population density fluctuates highly within the year but also between years (*e. g.* Fukuda *et al.*, 1983 and Miyazaki and Ishii, 2004). Indeed, the mean annual frequency of visits on Mt Katsuragi was 30.1 and 5.0/5 min/day in 2001 and 2002, respectively. In 2001, the many spiral flights with sometimes more than 2 contenders involved corresponded to the highest level of aggressivity and the percentage of intraspecific fights also significantly increased. Therefore, the territoriality observed on Mt Katsuragi during the peak phase of adult abundance (late May to late June) in both years but especially in 2001 was hard to understand.

L. celtis is univoltine, though partially bivoltine, in Japan and the timing of territoriality should correspond to the timing of copulation which seems to occur only in spring, for the overwintered adults (Fukuda *et al.*, 1983). However, as shown previously, aggressive chases in Katsuragi 2001 and 2002 occurred from late May to late June, *i. e.* during the active

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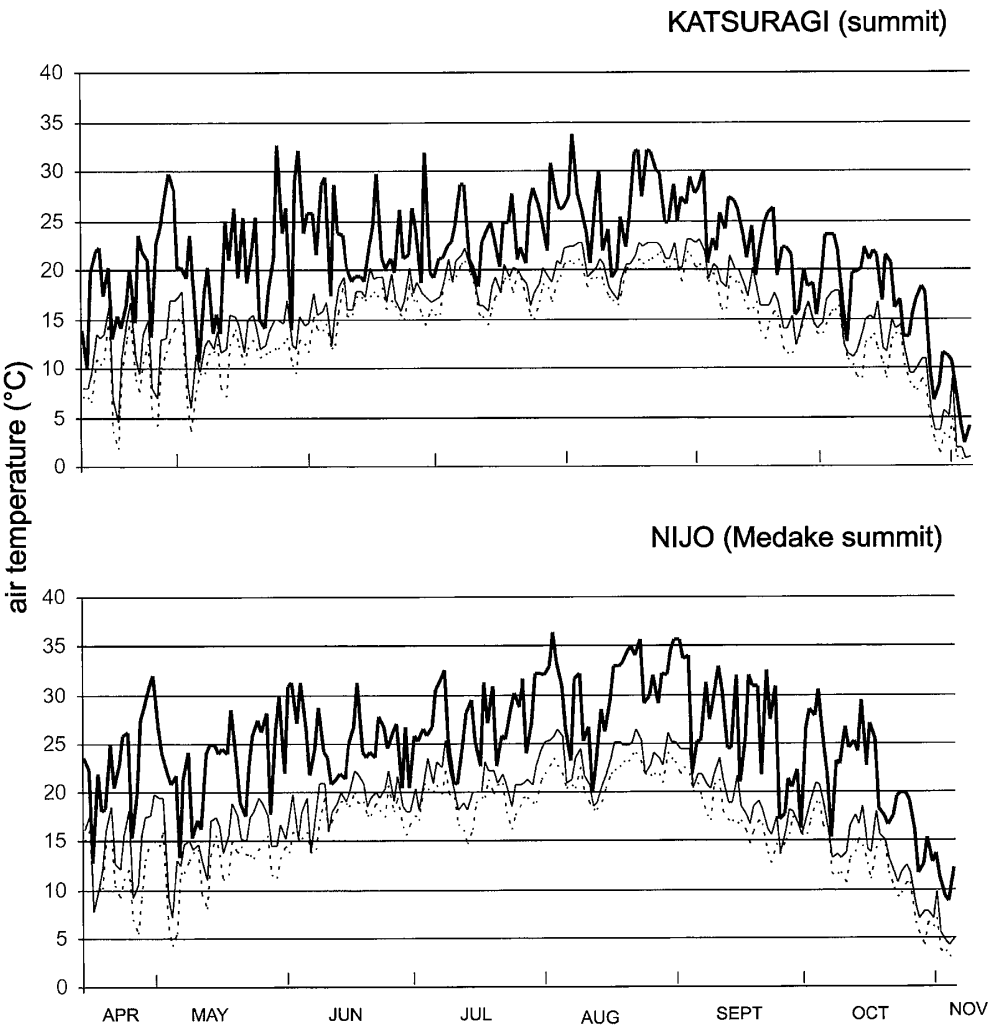

Fig. 2. Daily change of maximum and minimum air temperatures on two hilltops in 2003. Bold line=maxima; thin line=minima during the period covering the range of mate-locating activity for all species, namely from 8: 30 to 18: 30; dotted line=minima (over 24hr period).

phase after adult emergence and before aestivation. Therefore, the observed fights may be related to some purpose other than mating behavior, such as fighting for minerals from the ground when puddling in early summer or in relation to social behavior (Wynne-Edwards, 1965).

Nonetheless, territoriality of *L. celtis* was reported to occur in both individuals just after emergence and overwintering, around deciduous forests on forest edge canopies, by mostly perching on the foodplant, but also around vegetable fields (*e. g.* Fukuda *et al.*, 1983; Miyazaki and Ishii, 2004). This is a very different situation from the bare ground/grassy dominant vegetation on Mt Katsuragi's hilltop where no foodplant (*Celtis* spp.) is present. *L. bachmanii* also uses the larval foodplant as mate encounter site, with males perching on exposed branches and thus not on the ground (Rutowski *et al.*, 1997). Males of the African species, *Libythea labdaca*, also select territorial perches on the tops of trees (Williams, 1994).

Because of the three reasons just suggested, *L. celtis* may not be a real hilltopper in a narrow sense ("aggregation on summit for mating purpose") but only a seasonal migrant to

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Table 1. Classification of the different types of hilltopping and hilltoppers.

Hilltopping type	Purpose	Migrant	Hilltopper type	Frequency
A1 (narrow sense or "classical" type)	mating	no (*P. machaon*, spring *N. xanthomelas*, *L. japonica*, *A. hyperbius*, *H. japonica*) yes (*C. cardui*,*V. indica*, *L. boeticus*)	*P. machaon*, spring *N. xanthomelas*, *L. japonica*, *H. japonica*, *C. cardui*, *V. indica*, *L. boeticus*: strong (K, N and only K for *L. japonica* or N for *H. japonica*) *A. hyperbius*: moderate (K); strong (N)	regular
A2 (narrow sense)	mating (never percher and patrolling route through slopes)	no	*P. xuthus*: weak (N) *P. bianor, P. helenus*: weak (O)	regular
B	nectaring+mating+short stop	yes	*P. guttata*: moderate (K) *P. sita*: — (only short stop in K)	regular
C1	temporary habitat (aestivation including reproductive diapause for *L. celtis*)	yes (*L. celtis*) no (summer *N. xanthomelas*)	*L. celtis*: moderate (K, N) summer *N. xanthomelas*: strong (K)	regular
C2	temporary habitat (aestivation)+foodplant (*C. erate*, *P. sita*) +nectaring+mating. This combination: only in O for *P. sita*.	no (*C. erate*, *L. phlaeas*) yes (*P. sita*)	*C. erate*, *L. phlaeas*: moderate (K) *P. sita*: ? (O)	regular (*C. erate*, *P. sita*) occasional (*L. phlaeas*)

K = Katsuragi; N = Nijo; O = other mountains than K and N; "regular" means every year.

hilltops for other reasons. Indeed, *L. celtis* sometimes migrates and at least 3 libytheids, *L. bachmanni*, *L. carinenta* and *L. labdaca*, were recorded to make mass migrations (Williams, 1958). Although Fukuda *et al.* (1983) mentioned that the Japanese *Libythea* is not migrant in Japan, Ishii (2001) reported a mass migration of adult *L. celtis* in Northern Wakayama Prefecture in late May 1994.

12. *Colias erate*

On Katsuragi 2002 (Figs 1a–b), intraspecific chases, though not very aggressive, and thus probably only investigative, occurred on the summit and SubA and no perching, or only a trace of perching, was observed. It was thus a non-territorial patroller on Mt Katsuragi. In the pierids, low site tenacity and no site defense are the rule (Rutowski, 1991). More chases, including or not interspecific ones, occurred on SubA ($p<0.05$ and $p<0.01$, N=597, Chi-square tests) and more foraging on the summit than on SubA ($p<0.01$, $N=597$, Chi-square). A high proportion of courtships, relative to other species, was observed on the summit and SubA, with a somewhat higher percentage on SubA ($p<0.05$, $N=597$, Chi-square). On the summit, 18.0% ($N=383$) of female visits were recorded in 2002 and 19.9% ($N=306$) in 2001. By comparing with *A. hyperbius* (a classic, real hilltopper), the observed sex ratio of *C. erate* on the summit showed a high percentage of females and this tendency was the same in 2001. Since samples of the two species were of similar sizes, the bias coming from the fact that, during periods of low male density, the females are more easily noticed, due to in copula pairs being less rapidly formed than during periods of high male density (Shields, 1967), could not have played a role here.

On Nijo 2002 (Figs 1c–d), no chases and no perching were observed. *C. erate* was thus a

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non territorial patroller there. Only flying behavior and 1 courtship pair were observed on the summits on April 19, May 3, May 27 and May 29. The total number of visits on the summits was too small (Medake: 7 males and 5 females; Odake: 4 males and 7 females) though still fewer records were reported on the subsummit (2 flying males) and slope (2 flying males). Therefore, some slight tendency, though not statistically analysable, to aggregate also on Nijo's hilltops was apparent. On Medake and Odake summits respectively, 41.7% (N=12) and 63.6% (N=11) of female visits were found. Therefore, as on Mt Katsuragi, the sex ratio on Nijo's hilltops also showed a disproportionately high number of females for a hilltopper, comparatively to *A. hyperbius*. However, this time, the bias cited previously was certainly present because of the huge differences of sample sizes between the two species compared. This bias would also explain why the female proportion of *C. erate* was much higher on Nijo 2002 than on Katsuragi 2002 or 2001. Nonetheless, it cannot explain all existing contrasts between *C. erate* and *A. hyperbius* sampling sex ratios. In conclusion, on both mountains, *C. erate* exhibited a non classical pattern for a hilltopper in the sense of Shields (1967).

Since many females and courtships were observed on the hilltop of Mt Katsuragi, this constitutes a different pattern from a classical hilltopper where females are hardly seen and come only to the summit for the time of mating then fly downslope for oviposition. Therefore, females seemed to remain on the summit of Mt Katsuragi, which was a main breeding area for them. Indeed, the main foodplants and nectar sources, *Trifolium repens* and *T. pratense* (Fukuda *et al.*, 1982), were present in abundance. On Mt Katsuragi, the abundance of clovers may be close to lowland's and it seems thus quite unlikely that *C. erate* was a real hilltopper there (*i. e.* non-resource landmark mating system). However, many individuals of *C. erate* are known to gather on such high altitude mountains as Mt Shirane in Nikko, northern Kanto and a 1,600 m point of Akaishi Mountain Range (Fukuda *et al.*, 1982).

As a conclusion, *C. erate*, may only be a seasonal immigrant to the hilltops to avoid the Japanese summer heat in lowland areas. A comparison of seasonality data from Mt Nijo and Mt Katsuragi seem to support that hypothesis. Indeed, *C. erate* was only observed for a few days in spring (27 and 29 May) on Mt Nijo's summits while it was observed for a much longer period, spanning spring and summer, on Mt Katsuragi's (in 2001: from 29 May to 9 August; in 2002: from 8 April to 7 August). The longer stay on Mt Katsuragi's hilltop might be explained by its cooler climate (Fig. 2), since individuals were no longer present in summer on Mt Nijo.

13. *Lampides boeticus*

On Nijo 2002 (Figs 1c–d), intraspecific fights occurred on both summits and the proportion of perching there was much lower than flying (p<0.001, N=220 in Medake; p<0.001, N=60 in Odake; binomial tests). This species was thus a territorial, dominant patroller on both peaks. Only 3 records, all flying, were taken on the subsummit and no records on the slope.

On Katsuragi 2002 (Figs 1a–b), the occurrence of intraspecific fights on the summit and the dominant proportion of flying over perching (p<0.001, N=99, binomial test) implied that, as on Mt Nijo, it was a territorial, dominant patroller there. Intraspecific fights did not occur on the SubA and foraging was seen in equal proportion on the summit and SubA (p>0.05, N=163, Chi-square).

As a conclusion, on both mountains, it was a hilltopper in the sense of Shields (1967). It is also considered as a hilltopper in Fukuda *et al.* (1984), Pringle *et al.* (1994), and Shields (1967).

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14. *Lycaena phlaeas*

No reliable quantitative behavioral data on Katsuragi 2001 and 2002 were available and *L. phlaeas* adults were mainly distributed in a restricted zone of SubA. However, territorial perching and many intraspecific fights were observed in 2001, namely 22.5% of intraspecific fights (N=147) on the broad summit including SubA. It was especially the case at the level of one circle (SUB15) and the only mating pair observed was also found in the circle. There was a big concentration of flowers around circle SUB15 in July 2001. In 2002, no flower concentration was present there and the density of *L. phlaeas* was roughly one quarter of that recorded in 2001 (3.6/5min/day in 2001 *vs* 1.0 in 2002). In 2002, only 8.2% (N=85) of intraspecific fights occurred on the broad summit, which is significantly lower than in 2001 (p<0.01, N=232, Chi-square), and they were not concentrated in one particular circle of the subsummit. In 2002, 3 individuals were seen perching on flowers in circle SUB17 before fighting together.

All previous findings thus seem to corroborate Suzuki's (1976), namely that nectar sources remote from the larval foodplant are the encounter sites used by *L. phlaeas* for mate-locating (territorial perching). Almost no foodplants of *L. phlaeas* (*Rumex* spp., Polygonaceae) were present on the hilltop of Mt Katsuragi. A close relative, *L. hippothoe*, behaves similarly and it has been shown that fecundity in this species depends strongly on adult nectar resources (Fischer & Fiedler, 2001). However, this does not eliminate the question about the necessity of migrating to hilltops to find such flower concentrations. Since *L. phlaeas*, like *C. erate*, is a northern species, it might be a seasonal migrant to hilltops of sufficiently high mountains to escape from suboptimal high summer heat in the lowland. Mt Nijo, where *L. phlaeas* was not hilltopping despite the presence of flowers on Medake's hilltop, may be a too low mountain with temperatures on hilltops still close to those in the lowland (Fig. 2), though this is contradicted by Hiura (1976) who found an abundant density of *L. phlaeas* in the first part of summer on the top of Mt Nijo where nectaring sources were abundant. But, if this hypothesis is correct, it does not explain why this species only migrates and aggregates on hilltops occasionally, as indicated by 2002 *vs* 2001 results and the report of "sometimes flying to the summit" from Fukuda *et al.* (1984). This may be due to the obligatory presence of enough particular nectar sources on the hilltop of such high mountains, which can vary from year to year (*e. g.* 2002 results) or from mountain to mountain.

Even if the genus *Lycaena* may not comprise hilltopping species in North America, Shields (1967) cited the Lycaeninae as a subfamily containing hilltoppers (*e. g. L. sallustius*, an Australian species). Since *L. phlaeas* seemed to combine seasonal migration, *i. e.* the hilltop as a temporary habitat, with territories on nectar sources and nectaring, it was not a classical hilltopper in the sense of Shields (1967) and Alcock (1983) because the mate encounter site was different from a non-resource landmark mating system.

15. *Parnara guttata*

On Katsuragi 2002 (Figs 1a–b), on both summit and SubA, aggressive intraspecific chases occurred and almost no flying individuals were observed. It was thus a territorial percher there. However, aggressive chases were very few and in a higher proportion on SubA than on the summit (p<0.05, N=282, Chi-square). Besides, an extremely high percentage of foraging occurred on the SubA and, especially, on the summit (p<0.001, N=282, Chi-square), which was an "atypical pattern" for a hilltopper. Indeed, Shields (1967), showed that, even if feeding occasionally occurs on the summit during periods of the day when active hilltopping (*e. g.* perching, patrolling and chases) also occurs, the main feeding sessions of hilltoppers are separated in time from hilltopping behavior and occur somewhat more on the slope, subsummit or lowland than on the summit.

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As a conclusion from the results, *P. guttata* was not a typical or classical hilltopper in the sense of Shields' criteria. In our previous paper (Navez and Ishii, 2007), based on distributional arguments alone, there was doubt remaining whether this species is or is not a hilltopper. However, it was suggested to be a hilltopper by Ishii *et al.* (1986) and our behavioral data support their study. By checking the maturity of eggs and rate of copulation in females collected in different locations, Ishii *et al.* (1986) concluded that females seem to migrate from lowland emergence sites to the top of Mt Katsuragi for mating and that, just after copulation, there is a secondary dispersal to the lowland for oviposition. In their study, the mean daily sex ratio of *P. guttata* caught on the summit of Mt Katsuragi was 1:1, which sharply differs from the highly male-biased sex ratio on the summit for classical hilltoppers (Shields, 1967). This seems to be because this species combines migration with hilltopping. The purpose of hilltopping in *P. guttata* would thus associate mating and nectaring during migration, since few nectar sources are available around emergence sites in mid- and late summer (Ishii *et al.*, 1986).

Revised definition of hilltopper

In a traditional and narrow sense, species whose larvae pupate on or close to the larval foodplant, whose larvae and adults do not feed on a wide range of hosts, whose females lay eggs in batches (high synchronicity of eclosions), whose foodplants are either large (high density of larvae/plant) or patchily distributed (high density of foodplants), and whose breeding season is restricted in time, will not develop a hilltopping strategy (Rutowski, 1991). For instance, *C. cardui*, with a wide array of small size larval hostplants often pupates on a substratum other than the larval food plant and is a hilltopper (Rutowski, 1991). Other factors that concentrate receptive females in the landscape, such as dense patches of nectar sources and a patchy distribution of an essential thermal resource for receptive females (*e. g.* sunspots in the forest), will also prevent the evolution of hilltopping in those species (Rutowski, 1991; Fischer and Fiedler, 2001). In that sense, a species such as *L. celtis* which is only partially bivoltine and pupates mainly on larval foodplants of large size (*Celtis* trees) is not expected to be a hilltopper. *L. bachmanii*, a close relative with the same characteristics, uses the larval food plant as a mate encounter site (Rutowski *et al.*, 1997).

However, in a broader sense, species may use hilltops for many other purposes than mating (references in Shields, 1967; Samways, 1990) and, more interestingly, combine mating with those other purposes. Table 1 summarizes this diversity for all species envisaged in the present study and an additional species, *Parantica sita*.

By comparing male behavioral patterns of the hilltopping species from Mts Nijo and Katsuragi on summit, subsummit and slope, hilltoppers could be classified into 5 types (Types A1, A2, B, C1 and C2) with different purposes or a combination of several purpose(s). In some species a higher percentage of fighting occurred on the summit than on the subsummit and slope (Type A). In others, foraging was the dominant behavior on both summit and subsummit though fighting also occurred and somewhat more frequently on the subsummit (B). Finally, others were hilltopping in sufficient numbers only in summer and on peaks of relatively high altitude (C).

Type A species could be subdivided into 2: the first where some proportion of time was always spent perching on summit and subsummit (A1, such as *P. machaon*, spring adults of *N. xanthomelas*, *L. japonica*, *A. hyperbius*, *H. japonica*, *C. cardui*, *V. indica* and *L. boeticus*), the second where no perching occurred in any zone and with a relatively high percentage of visits on the slope (A2, such as *P. bianor*, *P. helenus* and *P. xuthus*). Similarly, Type C species were segregated into 2: the first with flying as the dominant be-

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havior, with fighting in equal proportions on the summit and subsummit (C1, such as *L. celtis* and the summer adults of *N. xanthomelas*), the second where courtship occurs in a non negligible proportion on both summit and subsummit with a relatively high percentage of foraging and fighting in both zones, though often higher on the subsummit (C2, such as *C. erate*, *L. phlaeas* and *P. sita*).

Type A has mating as a unique purpose, since fighting, among all behaviors compared, is the one with the strongest mating connotation. Type B species, such as *P. guttata* and *P. sita*, are exclusively migrant and combine 3 purposes: nectaring, mating and short stops on hilltops during their migrations. In Type C, hilltops are used as a temporary habitat during aestivation but, in Type C2, other purposes are also associated, such as breeding on the foodplant, nectaring and mating. Behavioral patterns were consistent between both mountains for the same species.

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摘　　要

大阪・奈良府県境の2つの山嶺の山頂, 亜山頂, 斜面における山頂占有性チョウ類の行動パターンの比較 (Sophie Navez ・石井　実)

2002年の4–10月に二上山と葛城山 (大和葛城山) の山頂, 亜山頂, 斜面において15種類の山頂占有性チョウ類の雄が示す各行動の頻度を調査することにより, 山頂占有性あるいは山頂占有者についてShields (1967) に基づく伝統的なものを補う新たな区分を提示した. 各行動の割合は, 葛城山に22箇所, 二上山に26箇所, それぞれ標高の異なる区域に設定した半径5 mの円形の定点において5分間当たりに観察された静止, 飛翔, 種内・種間闘争, 採餌などの雄の行動パターンの比率に基づいて評価した. この研究では, A1, A2, B, C1, C2という5つのタイプの山頂占有性行動を区別した. タイプA1の種は, 狭義の, あるいは「古典的な」山頂占有性チョウ類で山頂を配偶場所としてのみ利用していた. タイプA1には, キアゲハ, ギフチョウ, ツマグロヒョウモン, ヒメアカタテハ, アカタテハ, ヒオドシチョウの越冬成虫, ゴマダラチョウ, ウラナミシジミが含まれた. ナミアゲハ, カラスアゲハ, モンキアゲハのようなタイプA2の種は, タイプA1と同様の目的で山頂を利用するが, 静止することがなく, 斜面を通過する蝶道を形成していた. イチモンジセセリなどのタイプBの種は, 山頂を吸蜜, 配偶, 移動中の着陸場所の3つの目的で利用していた. テングチョウやヒオドシチョウの夏の成虫などのタイプC1の種では, 山頂はテングチョウの生殖休眠を含む夏眠期における, 低地の夏季の暑さを逃れるための一時的な生活場所として使われていた. 最後に, モンキチョウやベニシジミのようなタイプC2の種では, 夏眠期における一時的な生活場所として使われるだけでなく, 吸蜜や配偶, モンキチョウにおける寄主植物周辺での繁殖など, 他の目的も関係していた.

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